

Terminal phalanges in ranoid frogs: morphological diversity and evolutionary correlation with climbing habits

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We provide a descriptive survey of the morphological diversity of the shape of terminal phalanges of fingers and toes in ranoid frogs, based on analysis of 124 species of 64 genera, belonging to the Arthroleptidae (including Arthroleptinae, Astylosterninae and Leptopelinae), Brevicipitidae, Ceratobatrachidae, Dicroglossidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Phrynobatrachidae, Ptychadenidae, Puzoscephalidae, Ranidae and Rhacophoridae. For comparative purposes, specimens of 26 species of 18 genera belonging to ten non-ranoid frog families were also surveyed. The bones were analysed macroscopically as well as using scanning electron microscopy. Terminal phalanges were classified into 13 character states, called A to M, and into three major character state groups: (I) pointed tips, (II) rounded and relatively broad tips, (III) bifurcated tips. Eight character states were observed within ranoids, and six of these also occurred in non-ranoid taxa; five further states were found exclusively in the non-ranoid taxa. In order to assess homoplasy and possible adaptive significance for this osteological character, we compiled, from recent molecular studies, a consensus tree of the ranoid genera studied here. Tracing the evolution of all character states along this phylogeny was largely ambiguous but became more feasible when summarizing character states of distally enlarged (bifurcated or mushroom-shaped) vs. non-enlarged phalanges. Non-enlarged phalanges were supported as ancestral states in most clades, and an independent evolution towards distally enlarged phalanges was indicated in 12 clades, plus two reversals and two ambiguous transformations. Concentrated-changes tests supported a significant association of the evolution of distally enlarged phalanges with climbing habits, indicating an important adaptive component that likely explains the high degree of homoplasy in this skeletal character.

INTRODUCTION

At deep phylogenetic levels, amphibians show a high degree of morphological homoplasy (e.g. MULLER *et al.*, 2004; VAN DER MIJDEN *et al.*, 2005). Especially frogs are

characterized by a highly derived *bauplan* that possibly allows only a limited number of general variations in order to adapt to certain ecological niches (EMERSON, 1986). For instance, arboreal frogs in families that belong to different major clades can be extremely similar externally, characterized by a broad head with large eyes, enlarged terminal pads on fingers and toes, and often also other characters such as extended webbing between toes and sometimes fingers, a smooth dorsal skin without longitudinal folds, or the lack of a sharp border between dorsal and lateral colour. Neotropical species of the Hylidae can be so similar to Asian species of the unrelated Rhacophoridae that a familial diagnosis is merely impossible without examining osteological features such as shoulder girdle structure or the form of the terminal phalanx bones of fingers and toes. Sand frogs (the genus *Tomopterna* in the family Ranidae) were long believed to contain African as well as Asian and one Madagascan species based on their external similarity, but molecular work (BOSSI UT & MILINKOVITCH, 2000, VENCES & GLAW, 2001) demonstrated that the three geographic assemblages belong to different and not closely related clades, namely the African *Tomopterna* to the Pyxicephalidae, the Asian species (as genus *Sphaerotheca*) to the Dicroglossidae, and the Madagascan species (as *Laliostoma labrosum*) to the Mantellidae. Among African frogs, recent molecular work (VAN DIR MEIJDEN et al., 2005; FROST et al., 2006) highlighted an endemic clade, the Pyxicephalidae, that in addition to *Tomopterna* contains a variety of other anuran genera of such diversity that before they had been classified into five different subfamilies.

Whereas general external morphology of frogs is certainly subjected to strong homoplasy, osteological features are usually attributed important value for reconstructing anuran phylogeny. In fact, several character states such as a firmisternal shoulder girdle are well suited to define certain derived clades of frogs, for example the Ranoidea. However, many of these states have evolved convergently in other clades of the amphibian tree e.g., the firmisternal shoulder girdle in dendrobatids, atelopodine bufonids and pipids. Similar to external characters, several features of shoulder girdle morphology are probably under selective pressure as they may be relevant for locomotion, such as the shape of the omosternum (forked or unforked), the ratio of omosternum/sternal style length, or the general arciferal or firmisternal state (EMERSON, 1983). The same may apply to most other osteological features of anurans, but detailed analyses of functional morphology of these elements are surprisingly rare.

A further example for homoplasy in frog osteology is found in the presence of an intercalary element between the terminal and the penultimate phalanx of fingers and toes, a character first described by LYTIG (1876) in *Hyla arborea*. It has been considered of great phylogenetic value to define Old World tree frogs (e.g., LIU, 1970), but it is now clear that this element evolved convergently in at least the Hyperolidae, Arthroleptidae (genus *Leptopelis*), Rhacophoridae/Mantellidae, Microhylidae (genus *Phrynomantis*), Centrolenidae and Hylidae, and possibly reversed in one mantellid clade (genus *Laliostoma*).

Nevertheless, early studies of anuran systematics and phylogeny were largely based on osteological features (e.g., NÖBL, 1931; PARKER, 1934; LAURENT, 1940, 1941a-b, 1943a-b, 1944). In ranoid frogs, LIU (1970) studied the phylogeny of Old World treefrogs based on 36 characters, 14 of which were osteological characters of the skull, vertebrae, pectoral girdle, hyoid skeleton, carpals, tarsals, metacarpals and terminal phalanges. CERRI (1981) examined 22 osteological characters of the skull, pectoral girdle, vertebrae, ilium and the terminal

phalanges in African ranids; and DREWES (1984) studied 30 morphological characters of which 21 osteological characters of the skull, pectoral girdle, hyoid apparatus, carpals, tarsals and terminal phalanges. CHANNING (1989) combined and re-analyzed the data of LIEM (1970) and DREWES (1984). More recently, SCOTT (2005) studied 178 morphological characters, 101 of which were osteological. Several other studies have focused on particular osteological characters and analyzed their variation in specific groups of ranoid frogs, or across frogs in general, including ranoids (e.g., LAURENT & FABREZI, 1985, 1990; FABREZI & ALBLRCH, 1996; FABREZI & EMERSON, 2003; MANZANO et al., 2007).

One of the characters used in all these studies is the shape of the terminal phalanx bones of fingers and toes (see also DECKERT, 1938; THEIN, 1965; PERRET, 1966; LYNCH, 1971; HEYLER, 1975). However, the numbers and definitions of states described for this character were different, with LIEM (1970) and DREWES (1984) recognizing four states, CLARKE (1981) recognizing seven states, and SCOTT (2005) recognizing three states in the fingers and seven states in the toes. Variability in the phalanx shape within individuals has been noted (HEYLER, 1975; CLARKE, 1981), an adaptive value of this character postulated (DREWES, 1984), and problems in a clear categorization in character states emphasized (CLARKE, 1981). FABREZI (1996) undertook a wide survey of these characters in various neobatrachian frog lineages and observed a high degree of homoplasy in these bones, both regarding shape and development.

In this paper, we undertake a wide survey of the morphology of terminal phalanx shape in frogs, mainly focusing on ranoid frogs. This group corresponds to the superfamily Ranoidae as understood by DU BOIS (1992, 2005), with a taxonomic content similar to the unranked taxon "Ranoides" created and defined by FROST et al. (2006).

Based on examination of cleared and stained specimens and scanning electron microscopic pictures, we provide detailed descriptions of the variation observed in this state. We further analyse the evolution of this character along an informal supertree of these frogs based on recent molecular studies, and use comparative methods to test for the influence of the general ecological habits on this skeletal character.

MATERIAL AND METHODS

This study is based on an analysis of 124 species of 64 genera, belonging to the following ranoid families as recognized by FROST et al. (2006), Arthroleptidae (including Arthroleptinae, Astylosterninae and Leptopelinae), Brevipitidae, Ceratobatrachidae, Dicroglossidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Phrynobatrachidae, Ptychadenidae, Pyxicephalidae, Ranidae and Rhaecophoridae. For comparative purposes, also specimens of 26 species of 20 genera belonging to ten non-ranoid frog families were surveyed. Altogether, we screened cleared and stained skeletons of 190 ranoid and 29 non-ranoid specimens. The appendix provides a list of all specimens that were examined, with the collections where they are deposited.

The family-level classification used herein follows almost fully the recent proposal by FROST et al. (2006). This work certainly constitutes a great progress in anuran systematics, especially because an overdue partitioning of several large, heterogeneous and partly not

monophyletic families has been undertaken by these authors. On the other hand, several of the new arrangements, such as sinking the Leptopelinae and Astylosternidae in the family Arthroleptidae, or the Nasikabatrachidae into the Sooglossidae, may have been premature and recognition and revalidation of a few additional families will probably be a theme in future studies of anuran systematics. However, since such proposals are far beyond the scope of the present paper, we here follow the family-level taxonomy proposed by FROST et al. (2006), with a few exceptions only (we recognize the Astylosterninae as a subfamily of the Arthroleptidae, and continue using the genus name *Phrynodon*, to make it easier to refer to these frogs in the text), and we continue accepting Laliostominae as a mantellid subfamily (see GLAW & VENCES, 2006, GLAW et al., 2006). Species belonging to the following genera have been studied: *Afraxalus* Laurent, 1944; *Agalychnis* Cope, 1864; *Aglptodactylus* Boulenger, 1919; *Ameerega* Bauer, 1986; *Anodonihyla* Müller, 1892; *Arthroleptis* Smith, 1849; *Astylosternus* Werner, 1898; *Batrachylodes* Boulenger, 1887; *Blommersia* Dubois, 1992; *Bombina* Oken, 1816; *Boophis* Tschudi, 1838; *Breviceps* Merrem, 1820; *Cacosternum* Boulenger, 1887; *Caluella* Stohczka, 1872; *Ceratobatrachus* Boulenger, 1884; *Chromantis* Peters, 1854; *Colostethus* Cope, 1866; *Cophixalus* Boettger, 1892; *Cophyla* Boettger, 1880; *Dendrobates* Wagler, 1830; *Dermatonotus* Méhely, 1904; *Discoglossus* Otth, 1837; *Epipedobates* Myers, 1987; *Euphyctis* Fitzinger, 1843; *Fejervarya* Bolkay, 1915; *Gastrophryne* Fitzinger, 1843; *Gephyromantis* Methuen, 1920; *Gubemantis* Dubois, 1992; *Heleophryne* Selater, 1898; *Hemisus* Günther, 1859; *Heterixalus* Laurent, 1944; *Hoplobatrachus* Peters, 1863; *Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991; *Hyla* Laurenti, 1768; *Hylarana* Tschudi, 1838; *Hymenochirus* Boulenger, 1896; *Hyporolus* Rapp, 1842; *Kaloula* Gray, 1831; *Kassina* Girard, 1853; *Kurixalus* Ye, Fei & Dubois, 1999; *Laliostoma* Glaw, Vences & Bohme, 1998; *Leptodactylodon* Andersson, 1903; *Leptopelis* Günther, 1859; *Limnodrynastes* Fitzinger, 1843; *Limnometes* Fitzinger, 1843; *Lithobates* Fitzinger, 1843; *Mantella* Boulenger, 1882; *Mantidactylus* Boulenger, 1895; *Megophrys* Kuhl & Van Hasselt, 1822; *Microhyla* Tschudi, 1838; *Nanorana* Günther, 1896; *Natalobatrachus* Hewitt & Methuen, 1912; *Ociodozyga* Kuhl & Van Hasselt, 1822; *Odorana* Fei, Ye & Huang, 1990; *Oophaga* Bauer, 1994; *Petropedetes* Reichenow, 1874; *Phlyctimantis* Laurent & Combaz, 1950; *Phrynobatrachus* Günther, 1862; *Phrynodon* Parker, 1935; *Phrynomantis* Peters, 1867; *Pipa* Laurenti, 1768; *Platymantis* Günther, 1859; *Polypedates* Tschudi, 1838; *Pseudophryne* Fitzinger, 1843; *Ptychocheilus* Boulenger, 1917; *Quisipua* Dubois, 1992; *Rana* Linnaeus, 1758; *Rhacophorus* Kuhl & Van Hasselt, 1822; *Rhoderma* Duméril & Bibron, 1841; *Scaphophryne* Boulenger, 1882; *Scotohleps* Boulenger, 1900; *Silurana* Gray, 1864; *Sphaerothera* Günther, 1859; *Spmomantis* Dubois, 1992; *Stanois* Cope, 1865; *Strongylopus* Tschudi, 1838; *Tachycnemus* Fitzinger, 1843; *Tomopterna* Duméril & Bibron, 1841; *Tribatrachus* Boulenger, 1900; *Xenopus* Wagler, 1827

Clearing and staining was carried out according to standard protocols (DINGRICKS & UHLIR, 1977) as modified by PLOSC (1991). The third finger and the fourth toe are generally the longest digits, and terminal phalanx morphology is usually best expressed in these digits, although terminal finger phalanx morphology does not necessarily correspond with that of the toes (CLARK, 1981). Except for a few specimens where the hand bones were disconnected and a precise identification was not possible, the present study is focused on a comparison of the terminal phalanx of the third digit of the hand. This bone was drawn under a stereo microscope equipped with a camera lucida, mostly from the dorsal side. The drawings were used to attain a preliminary categorisation of character states. On this basis, we selected

representative specimens for each state for closer examination by scanning electron microscopy (SEM). Further SEM analyses were carried out on specimens where the character states could not be reliably scored otherwise.

The terminal and the penultimate phalanges of the third finger were removed from the cleared and stained specimens. Tissue remains were then dissolved in KOH, the bones prepared for SEM analysis using standard gold-coating procedures, and studied using a JEOL 35C microscope. The species and specimens for which the terminal phalanx of the third finger (unless mentioned otherwise) has been SEM-pictured are indicated in the appendix and most SEM pictures are reproduced in fig. 1-8. In the following species, other terminal phalanges were SEM pictured. *Fejervarya cancrivora* (also fourth toe), *Gastrophryne* cf. *olivacea* (only fourth toe), *Kassina decorata* (also fourth toe), *Phrynobatrachus mababiensis* (fourth toe), *Phrynobatrachus werneri* (only fourth toe), *Phrynodon* cf. *sandersoni* (several terminal phalanges, also first and second finger), *Pipa carvalhoi* (third toe), *Pseudophryne hiberni* (bones disconnected, differentiation between fingers and toes impossible), *Ptychadena mascareniensis* (also fourth toe, ZFMK 55157), *Scaphiophryne brevis* (only fourth finger as the other fingers were missing), *Strongylopus grayi* (only first finger, as the other fingers were disconnected), *Trichobatrachus robustus* (two specimens, the biggest specimen had an extra hook on top of its phalanx which has been pictured as well) and *Xenopus victorianus* (also third toe and fifth finger)

To test for a correlation among climbing habits and shape of terminal phalanges, we transformed these into binary characters (climbing vs. non-climbing, and distally bifurcated vs. non-bifurcated) and traced ancestral character states using both *Acctan* and *Deltran* models in MacClade (MADDISON & MADDISON, 1998). We used the concentrated-changes test of MADDISON (1990) to test the association of changes in these two binary characters (see LORCH & EADIE, 1999). This test determines the probability that various numbers of gains and losses of the dependent variable (terminal phalanx morphology) would occur in certain distinguished areas of the clade selected (defined by climbing habits), given that a certain number of gains and losses occur in the whole clade, and given the null model that changes are randomly distributed among the branches of the clade.

RESULTS

Based on this study, we distinguish a total of 13 character states for the shape of the terminal phalanx of the third finger, named A to M and classified into three major character state groups: (I) pointed tips, (II) rounded and relatively broad tips, (III) bifurcated tips. An additional state, the hook-shaped morphology, was only observed on the terminal phalanges of the toes and it is therefore not coded. Considerable variation was found within species of the same genus, e.g. in *Scaphiophryne* (*S. brevis*, state E, *S. calcavata*, state F, and *S. marmorata*, state H). In some cases, a limited amount of variation was also observed between individuals of the same species. Descriptions of character states given in the following refer largely to the dorsal view, with more complete descriptions from different angles for those species for which SEM pictures were made. For each character state we list the taxa that fit that description, with all deviations from the typical state described in more detail. In species

where phalanx morphology of all or some toes was very different from that of the third finger, we give short descriptions also of the deviant toe phalanx morphology

CHARACTER STATES

State A

From the basis, the terminal phalanx becomes less broad towards the (rounded) tip, which does not end in a bulb. Sometimes the tip is somewhat pentagonal or tetragonal. Observed in: *Afrivalus delicatus*, *A. fornasini*, *A. fulvovittatus* and *A.* sp. (fig. 1a), *Fejervarya cancrivora* (fig. 1c1-d3) and *F. limocharis*; *Heterivalus alboguttatus*, *H. andrakata*, *H. betsi-leo*, *H. luteostriatus*, *H. madagascariensis*, *H. punctatus*, *H. rutenbergi*, *H. tricolor* and *H. variabilis*, *Hyperolius argus*, *H. marmoratus*, *H. nasutus*, *H. pusillus*, *H. semidiscus*, *H.* sp. and *H. tuberilinguis*, *Leptodactylodon mertensi*; *Leptopelis bocagii*, *L.* cf. *mossambicus*, *L. modestus*, *L. natalensis* and *L. rufus*; *Megophrys nasuta*, *Ociodryga lima*, *Phyllomedusa sauvagii*

The terminal phalanx of the *Afrivalus* species studied ends in a pentagonal tip. In both *Fejervarya* species the terminal phalanx of the toe is relatively long. The tip of the terminal toe phalanx is bent towards the ventral side, ending in a small bulb that cannot be recognized from the dorsal side. A bulb at the terminal tip is also present at the fingers, seen from the dorsal side. This small bulb indicates that *Fejervarya* could also fit state F. Seen laterally, the dorsal side of the terminal phalanx is straight, and the ventral side makes an S-curve from the basis towards the tip (fig. 1c1-d3). This S-curve is absent in other genera categorized in state A, although it is typically found in species with a hook-shaped morphology. *Hyperolius* and *Heterivalus* share the same terminal phalanx morphology. In *Leptodactylodon mertensi*, the terminal phalanges of toes and fingers are similar. In *Ociodryga lima*, the tip of the terminal phalanges is somewhat pentagonal as in *Afrivalus*.

State B

This form has only been observed in *Pipa carvalhoi*. The terminal phalanx tip is rounded and not stretched laterally, although it has a protuberance sticking out on top. All fingers are of identical morphology. The toes are similar to state E as described below; the terminal phalanx tip is not perfectly round but a little bumpy.

State C

This form has only been observed in *Xenopus victorinus* (fig. 1c). The terminal phalanx tips of the fingers are split in three. The terminal phalanges of the fourth and fifth toe have two tips without a distinct ridge in between, as if the terminal phalanx tip had been excavated. The terminal phalanges of the first, second and third toe bend towards the ventral side and end in a sharp point, with a tendency towards a hook-shaped morphology.

State D

The phalanx tip is a highly reduced form, found in *Lumadonastes* sp. only. Since no SEM picture was made, further comparisons are not possible.

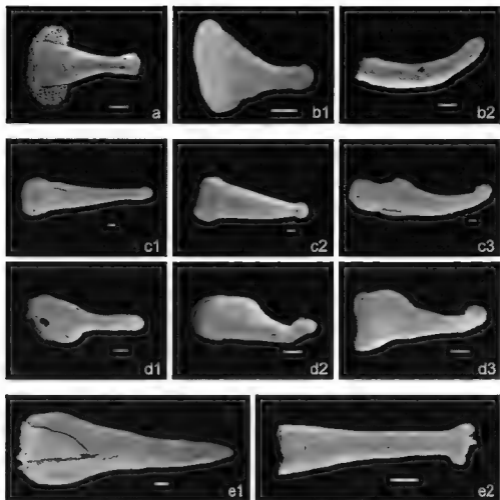


Fig. 1. Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned), categorized in morphological states A, A/F and C: (a) *Afryalus* sp., ventral view, state A; (b1-2) *Leptopichis natalensis*, dorsal and lateral views, state A; (c1-3) *Fejervarya cancrivora*, dorsal, ventral and lateral views, state A/F; (d1-3) *Xenopus victorinus*, fourth toe, dorsal, lateroventral and lateral view, state C; (e1) *Xenopus victorinus*, fourth toe, dorsal view, state C; (e2) *Xenopus victorinus*, dorsal view, state C. The scale bars represent 100 μ m.

State E

The tip of the terminal phalanges has no conspicuous shape. It is rounded and slightly cone-shaped, lacking a clearly defined knob or bulb at the end.

The following species are categorized in this state: *Aelptodactylus madagascariensis* (fig. 2c), *Breviceps fuscus* and *B. mossambicus* (fig. 2a), *Discoglossus galganoi*, *Hemisus*

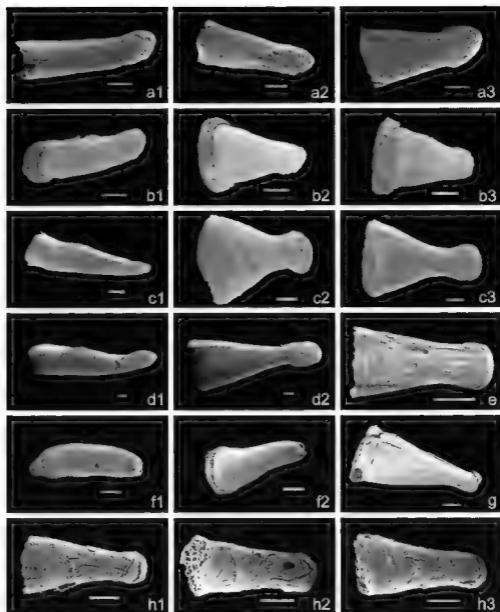


Fig. 2. – Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state E. (a1-3) *Breviceps mussambicus*, lateral, lateroventral and dorsal views, (b1-3) *Scaphiophrynus brevix*, lateral, dorsal and ventral views (c1-3) *Lablostoma labrosan* (Zf MK 59967), lateral, ventral and dorsal views, (d1-2) *Lablostoma labrosan* (Zf MK 8890), lateral and dorsal views, (e) *Aglyptodontis madagascariensis*, dorsal view, (f1-2) *Ptychoadena mascareniensis*, lateral and dorsal views; (g) *Platymantis coringatus*, dorsal view, (h1-3) *Pseudophryne hibroni*, finger number unknown, dorsal and ventral views, and dorsal view of another finger of the same individual. The scale bars represent 100 μ m

marmoratus, *Hoplobatrachus chinensis*; *Hyla arborea* and *H. cinerea*; *Lahostoma labrosum* (fig. 2c and 2d), *Platymantis corrugatus* (fig. 2g). *Pseudophryne bibroni*; *Ptychadena* cf. *mascareniensis*, *P. mascareniensis* (fig. 2f), *P. bibroni* (fig. 2h); *Scaphiophryne brevis* (fig. 2b).

In *Aglyptodactylus*, the phalanx tip has a very vague bump at the terminal tip. It is almost a straight line from basis to the tip of the terminal phalanx, only very slightly curved where the bulb/knob would start in state F. *Breviceps* are only tentatively categorized in this state since they show the most reduced form of terminal phalanges of all the species examined. In *Discoglossus galganoi*, the toe phalanges are longer than those of the fingers, but both have an equally rounded tip. In *Hemisus marmoratus*, the toes and fingers have the same shape of terminal phalanges. The two available specimens differ slightly in form. One has phalanx tips that are not shaped in any particular form, rounded and a bit cone-like, without knob form at the end. The tips of the terminal phalanges of the second specimen are also cone-like, but with a highly reduced knob at the end, hence fitting better in state E than in state F. In *Lahostoma*, terminal phalanges are distally with a slight constriction, creating a slight bulb at the tip, which is not obvious enough to place the species in state F. In *Platymantis corrugatus*, from the basis of the terminal phalanx towards the tip, the phalanx becomes narrower. It is most narrow at the point where in state F a constriction would be present. Except for *P. schullikorum*, which is categorized within state F, all *Ptychadena* species studied are categorized within state E, tending towards the morphology of state F. The terminal phalanges tips of the toes of *Ptychadena bibroni* have a hook-shaped morphology. In one of the specimen of *Ptychadena mascareniensis*, the tip does not end in a sharp hook but more pointed.

State F

The distal end of the terminal phalanges is cone-like, generally relatively broad, with a "knob" of various sizes at the end, in some cases with a constriction separating the knob from the remaining phalanx. The following species are categorized in this state: *Astylosternus montanus*, *Bombina* sp., *Cacosternum boettgeri* (fig. 3c); *Calluella guttulata*; *Ceratobatrachus guentheri* (fig. 3b), *Dermatonotus muelleri*, *Euphlyctis ehrenbergi*, *Fejervarya limnocharis* and *F. camerivora*; *Limnodynastes kuhlii*; *Lithobates catesbeianus*; *Microhyla pulchra*; *Nanomana pleskeri*; *Occidozyga martensii*; *Ptychadena schullikorum*, *Quasipaa spinosa*; *Scaphiophryne calcarata* (fig. 3a), *Scotobleps gabonensis*; *Sphaerotheca brevipes*, *Tomopterna delalandii* and *T. natalensis*; *Trichobatrachus robustus*.

In *Astylosternus*, the terminal phalanx of the third finger is not as broad as in most other genera placed within state F and ends in a relatively small knob. The terminal phalanges of the second, third, fourth and fifth toes have a hook-shaped morphology. In *Bombina*, the basis of the terminal phalanx is relatively broad, with a knob as broad as half the size of the basis. In *Cacosternum*, the phalanx is relatively narrow and elongated, with a knob at the distal end. In *Ceratobatrachus*, the phalanx is relatively broad at the basis, getting narrower towards the tip, and the tip ends in a small but distinct knob separated by a constriction that is about 1/3 as broad as the basis of the terminal phalanx. In *Dermatonotus*, the terminal phalanges are bent towards the ventral side. In *Euphlyctis*, the phalanx tip ends in a knob and the terminal phalanges of the toes are more elongated than the terminal phalanges of the fingers. In *Limnodynastes* and *Fejervarya*, the phalanx tip ends in a knob separated by a constriction. In the two juvenile specimens of *Lithobates catesbeianus*, the phalanx is not broad, but relatively

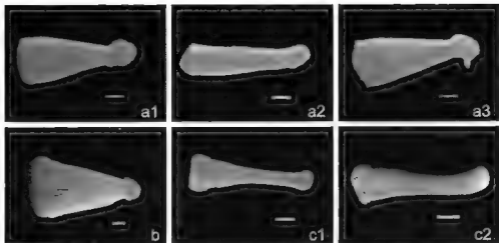


Fig. 3 Scanning electron microscope pictures of terminal phalanges of third finger. (a1-3) *Scaphiophryne calcarata*, dorsal, lateral and ventral views, (b) *Ceratobatrachus guentheri*, ventral view, (c1-2) *Cacosternum boettgeri*, dorsal and lateral views. The scale bars represent 100 μ m

long, ending in a bulb. In *Microhyla*, the knob expands slightly in lateral direction, making this a vaguely mushroom-shaped form tending towards character state M. In *Nanovana*, the phalanx is relatively long and narrow, ending in a knob separated by a constriction. In *Occidozyga martensii*, the terminal phalanges distally end in a knob separated by a constriction. *Ptychadena schillkorum* is an exception among the species of *Ptychadena*, which are otherwise categorized within state E. The examined specimen of *Scaphiophryne calcarata* has an anomaly on its lateral side on the distal end bulb. In *Scotobleps*, the terminal phalanges of the fingers are relatively long, not broad, and end in a small bulb. There are very slight lateral expansions, but these are too indistinct to be considered as representing a reduced form of state H. The terminal phalanges of the second and third toe have a hook-shaped morphology. The distal end of the first, fourth and fifth toe is rounded, but with lateral expansions, resulting in a mushroom-shaped form. In the species of *Sphaerotheria* and the two species of *Tomopterna*, in dorsal view, the terminal phalanx is broad at the basis. It has a clear bulb at the top, about half as broad as the basis. The phalanx is narrowest just before the knob, but a distinct constriction is lacking. In *Tichobatrachus*, the terminal phalanges of the fingers are cone-like and have a knob at the end. The terminal phalanges of the toes have a hook shape. In both specimens available, the hook-shaped morphology is present at all toes, however the biggest specimen has an extra, smaller hook on top of the hook-shaped toes. After dissolving the tissue with KOH, the extra, smaller hook appeared to be unconnected to the terminal phalanx (fig. 8a-b).

State G

The terminal phalanx is Y-shaped. Sometimes the two lateroterminal projections are slightly curved towards each other. The following species are categorized in this state,

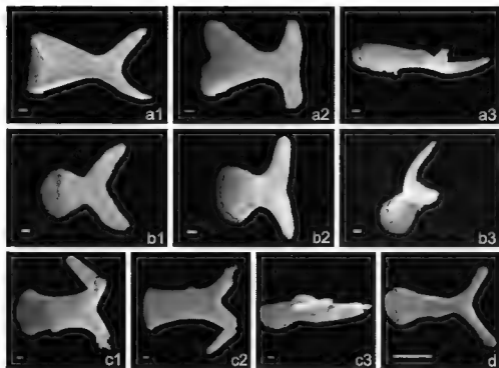


Fig. 4 Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state G (a1-3) *Anodonthyla montana*, dorsal, anteroventral and lateral views, (b1-3) *Phrynomantis bifasciatus*, dorsal and two ventral views (this species is categorized in state G, tending towards state J), (c1-3) *Rhacophorus demersi*, ventral, dorsal and lateral views (both tips of the terminal phalanx broken), (d) *Polypedates otlophus*, dorsal view. The scale bars represent 100 μm .

Anodonthyla montana (fig. 4a); *Cophyla phyllodactyla*, *Heleophryne regis*; *Phrynobatrachus avitatus*, *Phrynomantis bifasciatus* (fig. 4b) and *P. microps*; *Polypedates equus*, *P. maculatus* and *P. otlophus* (fig. 4d); *Rhacophorus demersi* (fig. 4c) and *R. nigropalmatus*.

In *Anodonthyla*, the two projections are slightly curved towards each other. A constriction was visible towards the end of the two projections on the SEM picture. In *Heleophryne*, sometimes the two projections are slightly curved towards each other. In *Phrynobatrachus avitatus*, the terminal projections are slightly less elongated. *Phrynomantis* has a slightly fish-tail shaped terminal phalanx, reminding of *Chromantis verampelina* and *Hylanana (Anmirana) cf. albolabris*, which are categorized in state J. The anterodorsal view shows a T-shaped morphology wherein the distal end is more or less in a straight line and the two projections extend in lateral direction. In some of the (juvenile) specimens of *Polypedates equus* examined, a constriction is visible towards the end of the two projections, comparable to *Anodonthyla montana*. In *Rhacophorus* the two projections are very narrow and in a straight line without curves.

State H

The terminal phalanges are T-shaped; at the distal end these form more or less a straight line. This state is similar to state G, only the two lateroterminal projections stretch away from each other in a more lateral direction. The following species are categorized in this state: *Batrachylodes elegans* and *B. vertebralis*; *Colostethus nubicola*; *Cophaxalus darlingtoni* and *C. riparius*; *Dendrobates auratus*, *D. leucomelas* and *D. tinctorius*; *Oophaga pumilio*; *Epipedobates boulengeri*; *Ameerega silverstonei*, *Phrynobatrachus* cf. *versicolor*, *P.* cf. *weneri* and *P. cricogaster*; *Kaloula pulchra*; *Kassina decorata*, *Natalobatrachus bonebergi* (fig. 5a), *Petropedetes* sp. (fig. 5b); *Phrynodon* cf. *sandersoni* (fig. 5c-e); *Scaphiophryne marmorata*; *Staurois* sp.; *Arthroleptus* [*Schoutedenella*] sp.

In *Colostethus*, the projections (distance between their tips) are as extended as the length of the whole terminal phalanx. In *Epipedobates* and *Ameerega*, the projections are a little more extended than the whole length of the terminal phalanx. In the three species of *Phrynobatrachus* included here, the projections are less extended, but still more than in state M. *Kaloula* has a morphology different from others that are placed within this state, the two projections are not stretching away from each other but the phalanges are distally fan-shaped and ending in a straight line. Also *Kassina* has a different morphology, as the two projections are much broader than in the other taxa placed within this state. *Phrynodon* cf. *sandersoni* sometimes has up to two distal protuberances on the phalanx tip. The place of occurrence varies from centrally to just left or right of the centre. This seems to vary not only randomly between the specimens, but also between fingers and toes, between left and right hand or foot, and even between digits of a hand or foot. In *Scaphiophryne marmorata*, the phalanges are T-shaped, the distal end forms a more or less straight line. The two projections stretch away in lateral direction. In *Arthroleptus* [*Schoutedenella*] sp., the terminal phalanges have a slightly reduced T-shape. The distal end forms more or less a straight line. The projections are less elongated than in other species in state H.

State I

The terminal phalanges are slightly Y-shaped. The two lateroterminal projections are not as prolonged as in state G but rather short and more closely connected with each other. This state is found in all examined species of the genera *Boophis* (fig. 6b), *Gephyromantis*, *Gubemantis*, *Mantella* and *Mantidactylus* (fig. 6a) which all belong in the Madagascan family Mantellidae; and in the rhacophorid *Kurixalus verrucosus*.

In *Boophis boehmeri*, *B.* cf. *madagascariensis*, *B.* sp. aff. *mbilans*, *B. idae*, *B. nmiatus* and *B. tephraeomystax* (fig. 6b), on the ventral side a "bump" can be seen, with an incision in the center. This bump is present in many other species as well, but without incision. In *Gephyromantis webbi*, *Gubemantis bicakaratius*, *G. flavobrunneus*, *Mantella aurantiaca*, *M. crocea*, *M. madagascariensis*, *Mantidactylus albofrenatus*, *M. grandisieri* and *M. ulerosus*, the two projections are slightly curved to the lateral sides (fig. 6a). In *Kurixalus verrucosus*, the morphology is similar to that of *Boophis tephraeomystax* (fig. 6b).

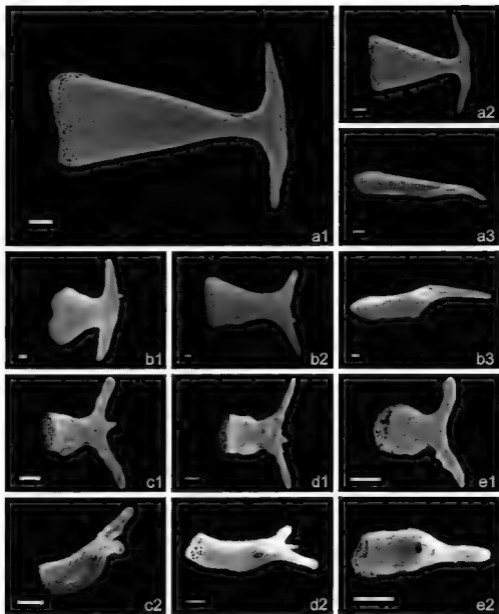


Fig 5 Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state H (a1-3) *Natalobatrachus bonebergi*, dorsal, ventral and lateral views, (b1-3) *Petropedetes* sp., anteroventral, dorsal and lateral views (the small bump on top of the terminal phalanx of *Petropedetes* is probably dust, it does not represent a characteristic feature of this taxon), (c1-2) *Phrynosoma* cf. *sandersoni*, dorsal and lateral views, (d1-2) *Phrynosoma* cf. *sandersoni*, dorsal and lateral views of first and second finger, (e1-e2) *Phrynosoma* cf. *sandersoni*, dorsal and lateral views of third finger. The occurrence and place of protuberances in this species varies, sometimes in the center, and sometimes just left or right of the center. The number of processes varies from none to two. This seems to vary not only randomly between the specimens, but also between fingers and toes, between left and right hand or foot, and even between digits of a hand or foot. The scale bars represent 100 μ m.



Fig. 6 Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned), categorized in states I, J, K and L (a1-2) *Mantidactylus ulerosus*, dorsal and anterodorsal views, state I, (b1-4) *Boopis tephraeom stav.*, ventral, dorsal and two anterodorsal views, state I, (c1-2) *Chromantis verampelna*, dorsal and lateral views, state J, (d1-d2) *Hyalinobatrachium fleischmanni*, ventral and lateral views, state K, (e1-e2) *Hymenochirus boettgeri*, postero-lateral and lateral views, state L, (f1-f2) *Agalychnis callidivus*, ventral and lateral views, state L (even though the terminal phalanges on some of these SEM-photographs are broken, they still give a good view of their morphology in *Hyalinobatrachium* and *Agalychnis*). The scale bars represent 100 μ m

State J

This state is expressed in a Y-form and can be described as a fishtail-shape. It is similar to state G, but with the two lateroterminal projections being enlarged. It has only been observed in *Chiromantis xerampelma* (fig. 6c) and *Hylarana (Amnirana) cf. albolabris*.

State K

This state is reminiscent of a combination of states G and H, but with the terminal phalanges being strongly elongated and becoming very narrow towards the tip. It has only been observed in *Hyalnobatrachium fleischmanni* (fig. 6d)

State L

The terminal phalanx is very narrow and relatively long, ending in a pointed tip. The distal end is slightly curved towards the ventral side.

This form has been observed in the following species. *Agalychnis callidryas* (fig. 6f), *Hymenochirus boettgeri* (fig. 6e) and *Silurana tropicalis*. In this latter species, the terminal phalanx of the first, second and third toe have a hook-shaped morphology. The terminal phalanx tips of the fourth and fifth toe are rounded and slightly cone-shaped. The terminal phalanx tips of the fingers are also sharply pointed, but not bent towards the ventral side.

State M

The phalanges show rudiments of bifurcation distally. This state does not describe a well-defined single morphology but is rather somewhat of a "dumpbin" for species of intermediate states or where different morphologies are observed among digits. The observed morphologies are: (1) the distal end of the terminal phalanx cone-shaped with a knob at the distal end that bifurcates and has a distinct median notch; (2) the distal end rounded but with lateral expansions, resulting in a mushroom-shaped appearance; (3) a reduced T form.

The following species are categorized in this state. *Arthroleptis adelphus*, *A. adolfriederici*, *A. poecilnotatus*, *A. sp* and *A. variabilis*; *Hylarana (Amnirana) lepus*, *Discoglossus montalentii*; *Discoglossus sardus*, *Gastrophryne cf. olivacea*; *Hylarana (Hydrophylax) galamensis*, *Hylarana (Hylarana) macrodactyla*, *Odorrana livida*, *Phlyctenmantis verrucosus*, *Phrynobatrachus mabubiensis*, *P. natalensis* and *P. werner*; *Rana dalmatina* and *R. temporaria*; *Rhinoderma darwini*; *Hylarana (Sylvirana) nigrovittata*, *Strongylopus gravii*; *Tachyvenemys seychellensis*.

Due to the large variability in the detailed expression of this state, we here provide brief descriptions for all taxa exhibiting it. In *Arthroleptis adelphus*, *A. adolfriederici*, *A. poecilnotatus*, *A. sp* and *A. variabilis*, the terminal phalanges shape varies. Distal ends can be bifurcated and have a distinct median notch, or have a mushroom-shaped morphology. In *Hylarana (Amnirana) lepus*, it bifurcates in lateral direction, mushroom-shaped. In *Discoglossus montalentii*, a strongly reduced T-shape is present both in fingers and toes. In *Discoglossus sardus*, the distal end of the terminal phalanx is cone-shaped with a knob at the distal end that bifurcates. There is no median notch, but the knob is not rounded either. The distal end

slightly looks cubical. In *Gastrophryne* cf. *olivacea*, two morphologies may occur on the same hand or foot without obvious order. The distal end of the terminal phalanx can be: (1) cone-shaped with a distinct median notch; or (2) rounded (fig. 7c). In *Hylarana* (*Hydrophylax*) *galamensis*, the terminal phalanx bends slightly towards the ventral side, ending in a bulb with two pointy tips, bifurcating in lateral direction. From an anteroventral angle, the curve in the phalanx tips causes an incomplete view and shows a mushroom-shaped form, with a lowering between the two bifurcating tips (fig. 7g). In *Hylarana* (*Hylarana*) *macroductyla* (two specimens), there is a highly reduced form of state H, bifurcating in lateral direction, without median notch. In *Odorrana livida* (two specimens), the terminal phalanx tips bifurcate in lateral direction. One of the two specimens has a mushroom-shaped bulb towards the ventral side (fig. 7a), whereas the other specimen extends a bit more laterally and tends to look more like the reduced form of state H. In *Phlyctmantis verrucosus*, two morphologies are observed: (1) the distal end of the terminal phalanx can be cone-shaped, bifurcating with a distinct median notch; or (2) the distal ends can be rounded, not shaped in any particular form. In *Phrynobatrachus mababiensis* (fig. 7e), *P. natalensis* (fig. 7d) and *P. werneri* (fig. 7f), the phalanges are relatively narrow and elongated and with various terminal tip morphologies. From the lateral side, the phalanx of *P. mababiensis* is straight with only the terminal tip bowing towards the ventral side. The broadened tip is divided into three parts on the anterior side, the central part of which is the shortest. The distal end of the terminal phalanx of *P. natalensis* is cone-shaped with a knob at the distal end that bifurcates and has a distinct median notch. The phalanx of *P. werneri* is slightly T-shaped tending to state H, as the two short projections extend in lateral direction and bend slightly in anterior direction. The top makes a straight line. The projections do not extend as far as in state H. Other species within the genus *Phrynobatrachus* (*P. auritus*, *P.* cf. *versicolor*, *P.* cf. *werneri* and *P. cricogaster*) are placed in states G, II-M, II-M and H respectively. In *Rana dalmatina*, the phalanx tip is mushroom-shaped. In *Rana temporaria*, the phalanx ends in a round mushroom-shaped bulb, which does not extend as much as other mushroom-shaped morphologies, tending towards state F. In *Rhinoderma darwini*, the distal ends of both fingers and toes are rounded, but with lateral expansions, resulting in a mushroom-shaped form. In *Hylarana* (*Sylvirana*) *nigrovittata*, the distal end is in a straight line and bifurcates in lateral direction. A highly reduced form of state H is observed in *Strongylopus grayii*, the distal ends are rounded with lateral expansions, resulting in a mushroom-shaped form (fig. 7b). In *Tachycnemis seychellensis* as in *Phlyctmantis*, two morphologies are observed: (1) the distal end of the terminal phalanx is cone-shaped, bifurcates and has a distinct median notch; and (2) the distal end is rounded, not shaped in any particular form.

MAJOR MORPHOLOGICAL GROUPS

Most of the different states defined above can be summarized in three major morphological groups, defined below. States B and C could not be placed in any of these groups, because their morphology is too aberrant. States D and M do not clearly fit in any of the groups either, and are possibly reduced forms of one of the other states.

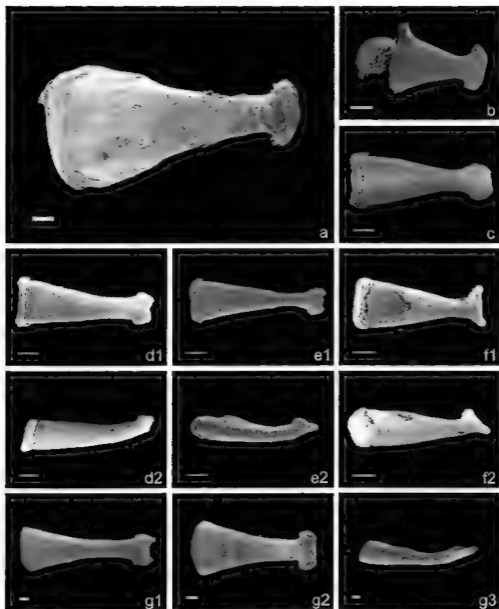


Fig. 7. Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned in the following), all categorized in state M: (a) *Odorrana livida*, ventral view, (b) *Strongylopus grayi*, dorsal view, (c) *Gastrophysone cf. olivacea*, dorsal view, (d1-2) *Phrynobatrachus natalensis*, dorsal and lateral views, (e1-2) *Phrynobatrachus nababiensis*, fourth toe, dorsal and lateral views, (f1-2) *Phrynobatrachus werneri*, fourth toe, ventral and ventrolateral views, (g1-3) *Hylarana / Hydrophylax galamensis* dorsal, ventral and lateral views. The scale bars represent 100 μ m.

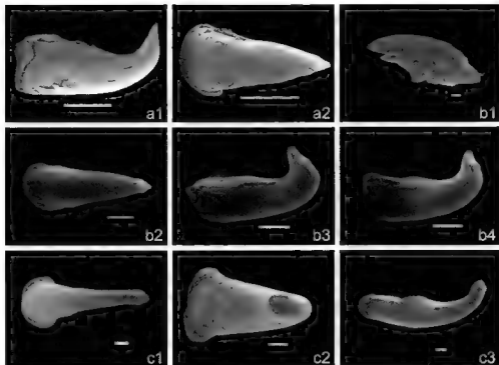


Fig 8 Scanning electron microscope pictures of terminal phalanges of fourth toe categorized as hook-shaped morphology (a1-2) *Trichobatrachus robustus* (ZFMK 68850), lateral and dorsal views, (b1) *Trichobatrachus robustus* (ZFMK 68851, hook on top of the terminal phalanx), lateral view, (b2-4) *Trichobatrachus robustus* (ZFMK 68851), dorsal, lateroventral and lateral views (the morphology of the third finger of *Trichobatrachus robustus* is categorized in state F). (c1-3) *Ptychadena mascareniensis*, dorsal, ventral and lateral views. The scale bars represent 100 μ m

Morphological group I

Pointed terminal phalanx tips, states A and L. *Afrivalus*, *Agalychnis*, *Fejervarya* (also state F), *Heterivalus*, *Hymenochirus*, *Hyperolius*, *Leptodactylodon*, *Leptopeltis*, *Megophrys*, *Occidozyga* (also state F), *Phyllomedusa* and *Silurana*

Morphological group II

Rounded and relatively broad terminal phalanx tips, states E and F. *Aglyptodactylus*, *Astytosternus*, *Bombina*, *Breviceps*, *Cacosternum*, *Calluella*, *Ceratobatrachus*, *Dermatonotus*, *Discoglossus*, *Euphlyctis*, *Fejervarya* (also state A), *Hemisus*, *Hoplobatrachus*, *Hyla*, *Lalostoma*, *Limnonectes*, *Lithobates*, *Microhyla*, *Nanorana*, *Occidozyga* (also state A), *Platymanis*, *Pseudophryne*, *Ptychadena*, *Quasipaa*, *Scaphiophryne brevis* and *S. cakanata*, *Scotobleps*, *Sphaerotheca*, *Tomopterna* and *Trichobatrachus*.

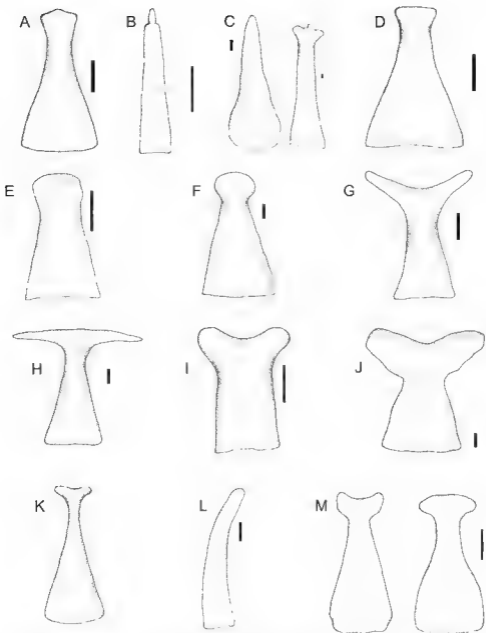


Fig. 9. Character states of terminal phalanx shape as distinguished in the present work. All drawings represent the third finger, except for the left drawing of character state C, which represents the fourth toe. The character state M includes phalanges with rudiments of distal bifurcation, and comprises different morphologies. Here, two examples are given of this character state. The morphologies can differ dependent on the observer's angle of observation. This is especially true for the drawing of character state A. What seems to be a slightly pointed head, is in fact a small bulb curving towards the ventral side (fig. 1a). The distal end of this bulb is rather flat than pointed. The scale bars represent 100 μm .

Morphological group III

Bifurcated terminal phalanx tips, states G, H, I, J and K: *Ameerega*, *Anodonthyla*, *Batrachylodes*, *Blommersia*, *Boophis*, *Chromantis*, *Colostethus*, *Cophixalus*, *Cophyla*, *Dendrobates*, *Epipedobates*, *Gephyromantis*, *Gubemantis*, *Heleophryne*, *Hyalinobatrachium*, *Hylarana* [subgenus *Ammirana*], (*Kaloula*), (*Kassina*), *Mantella*, *Mantidactylus*, *Natalobatrachus*, *Oophaga*, *Petropedetes*, *Phrynobatrachus* (some specimens in state M), *Phrynodon*, *Phrynomantis*, *Polypedates*, *Rhacophorus*, *Scaphiophryne marmorata*, *Arthroleptis* [*Schouteddenella*], *Spinomantis* and *Stauroids*.

CONSENSUS PHYLOGENY, CHARACTER TRACING AND CHARACTER CORRELATION

The systematics of ranoid frogs are still in a flux, but recent molecular work has clarified much of their basal phylogeny. We summarized molecular trees based on multi-gene analyses as published by BIJU & BOSSUYT (2003), ROELANTS et al. (2004), HOEGG et al. (2004), VAN DER MEIJDEN et al. (2004, 2005) and VENCES et al. (2003). We produced an informal supertree by manually superimposing these trees with molecular trees of deep amphibian relationships (SAN MAURO et al., 2005; ROELANTS & BOSSUYT, 2005), and considered nodes that received high support (Bayesian posterior probabilities > 95 % or bootstrap support values > 70 %) in at least one of the analyses and were not contradicted by highly supported alternative topologies in other analyses. A few additional aspects of the topologies were resolved following the analysis of FROST et al. (2006), although these authors did not provide bootstrap values which would have given a directly comparable measure of support to other analyses. Because of the limitations in including phalanx shape assessments published by other authors, we only included in the tree those genera for which terminal phalanx data were gathered in the present study. The resulting consensus tree is shown in fig. 10-11. Tracing character state transformations based on our original character states on this tree (not shown) required a minimum of 52 transformations and resulted in a consistency index (ci) of 0.38 and a retention index (ri) of 0.36. Tracing the three major groups of character states (not shown) required a minimum of 19 transformations and yielded values of ci/ri values of 0.11 and 0.48.

Reconstruction of ancestral states was ambiguous on these trees in most cases. In order to test for a possible correlation between habits and distal enlargement of the terminal phalanx, we divided the observed states in two major groups, namely (1) those without a distinct distal enlargement as in morphological groups I and II above (plus states D and M), and (2) those with a distinct Y-shaped, mushroom-shaped or T-shaped distal enlargement, as in morphological group III above. This character resulted in ci/ri values of 0.06 and 0.46, and a tree length of 16 transformations. Character tracing supported distally non-enlarged phalanges as the ancestral state in most major clades and supported an independent origin of distally enlarged phalanges in 12 clades (fig. 10). In at least two cases a reversal was indicated, and two further transformations could not be unambiguously identified as either origin or reversal.

We further grouped the genera studied grossly by their habits in non-climbing species (terrestrial, semi-aquatic and aquatic species) and climbing species (including arboreal, semi-arboreal and rock-dwelling taxa). This character resulted in ci/ri values of 0.05 and 0.40, and

a tree length of 19 transformations. Non-climbing habits were identified as ancestral and 11 independent origins of climbing habits were identified (fig. 11). Two reversals to non-climbing behaviour and five transformations of uncertain direction were further identified. Of the 11 origins of climbing, six coincided precisely with the origin of distally dilated phalanges. In several cases, this correlation seems obvious: (1) *Aglyptodactylus* and *Lahostoma*, clearly embedded in the Mantellidae/Rhacophoridae clade, are the most terrestrial mantellids and the only representatives in this family without distally enlarged terminal phalanges; (2) the most clearly rock-dwelling or scansorial ranoids, such as *Staurois*, *Natalobatrachus*, *Phrynodon* and *Petropedetes*, all have distally enlarged phalanges, (3) in *Scaphiophryne*, the one included species with enlarged finger disks and at least occasional climbing behaviour, *S. marmorata*, has distinct T-shaped phalanges, whereas the purely terrestrial species do not show any enlargement. Nevertheless, several striking counter examples exist as well, indicating that this correlation is certainly not an obligatory one: (1) the fully arboreal hylids show no distal enlargement, and (2) the same is true for the arboreal hyperoliids and leptopelins (paradoxically, except for the largely terrestrial *Kassina*).

For the concentrated changes test of character correlation as implemented in MacClade (using 10,000 simulations), it is necessary to trace ancestral states of dependent as well as independent variable as precisely as possible. In order to allow for unambiguous reconstructions, we therefore resolved the polytomies in our phylogeny as follows: (1) among microhylids, positioning *Phrynomantis* as most basal and gastrophrynines sister to microhylines; (2) among mantellines, placing boophines as most basal. It is highly unlikely that any alternative resolution of these polytomies would have affected the outcome of the concentrated changes test in a relevant way. Using *Deltran* character tracing, and under the null hypothesis that gains and losses are randomly distributed, the probability of observing, out of 13 gains and 4 losses, of the character state "bifurcated", the observed 7 and 0 (defined as more than 6 and less than 1), respectively, on branches distinguished by the character state "climbing", was lower than 0.005. Under *Acctran* reconstruction of ancestral states, 11 gains and 6 losses of bifurcated terminal phalanges were observed, 7 and 1 of which occurred in subclades characterized by a climbing character state ($P < 0.005$). Under MINSTATE and MAXSTATE simulations, the significances decreased, but the null hypothesis of randomly distributed changes (no correlation) was still significantly rejected ($P < 0.05$) in all cases.

DISCUSSION

COMPARISON WITH PREVIOUS STUDIES

In ranoid frogs, four authors (LILM, 1970; CLARKE, 1981; DREWES, 1984; SCOTT, 2005) have analysed the shape of terminal phalanges in detail and defined character states to be analysed in a phylogenetic context.

LILM (1970), in a study of Old World treefrogs (currently in the Hyperoliidae, Rhacophoridae and Mantellidae), recognized four states of the terminal phalanx (tab. 1), three of which compare directly to states E/F, G and I here. LILM's (1970) state I compares to a

Table 1. Character states of terminal phalanx shape as used by LIEM (1970) (first column) and their equivalents as defined here (last column).

State	State description	Compares to
0	Obtuse terminal phalanx, the distal end is simple or a rounded knob	States E and F
1	Claw-shaped terminal phalanx; pointed and curved downwards	Hook-shaped toe morphology
2	Bifurcate terminal phalanx; the distal end is slightly bifurcate but not pointed, and the length of each branch is less than the width of the phalanx	State I
3	Y-shaped terminal phalanx; the distal ends are pointed and the length of each branch is longer than the width of the phalanx	State G

hook-shaped morphology found in the toes of *Trichobatrachus robustus*, *Ptychadena bibroni*, *Astylosternus montanus*, *Scotobleps gabonensis* and *Siturana tropicalis* LIEM'S (1970) general observation of taxa currently in the Rhacophoridae and Mantellidae having Y-shaped or bifurcated phalanges corresponds well with the results obtained here.

CLARKE (1981) examined African species today classified in the Ranidae, Dicroglossidae, Ptychadenidae and Pyxicephalidae (FROST et al., 2006) and recognized seven different states of terminal phalanx shape. CLARKE'S (1981) states 1, 2 and 5 are reduced forms and were subsumed as state M in our study (tab. 2); state 0 compares to our state F and was found in species of Ranidae, in agreement with our observations of state M in *Hylarana* (*Hylarana*) *macrodactyla*, state 1 is comparable to our state M and was found in *Hylarana* (*Hydrophylax*) *galamensis* and *Strongylopus*, state 2 is also comparable with our state M and was found in *Aubria*, some species of *Comaua*, *Hoplobatrachus occipitalis* and *Pyxicephalus*. We did not study any of these taxa, and the precise form of this state according to CLARKE'S (1981) drawings was not observed by us in any other specimen, state 3, seen by CLARKE (1981) as extreme expression of state 2, was only observed in *Comaua beccarii* which we did not study here; state 4 is described as reduced and almost cone-like, and appears to best compare to our state E, it was found by CLARKE (1981) in *Tomopterna*, *Hildebrandtia* and *Pyxicephalus*, whereas we categorized *Tomopterna* in state F. CLARKE (1981) used a juvenile specimen of *Pyxicephalus adspersus* with incomplete ossification of the skeleton, which lead to doubt in showing state 2 or 4, state 5, comparable to state M in our study, was found in *Lanzarana lugeni* (not studied here), state 6 (comparable to our states A and L) was found in *Ptychadena* only, but according to our results, species of *Ptychadena* are characterized by a tendency towards a small terminal bulb and are therefore categorized in state E. Only *Ptychadena floereri* was not categorized in state E, but in state F. The pointed, dorsoventrally curved distal end in this species compares to a reduced form of a hook-shaped morphology, observed in this study in the phalanges of the toes of *P. bibroni*.

DREWES (1984) analysed the terminal phalanges of the third finger, mainly in hyperolids and leptopelins, but for comparative purposes also in other ranoids. He distinguished four states (tab. 3). State 0, from the drawings and descriptions provided, is comparable to the hook-shaped morphology, which in this study has only been observed in toes. State 1 compares to morphological group II, consisting of states E and F. The slightly notched

Table 2. Character states of terminal phalanx shape as used by CLARKE (1981) (first column) and their equivalents as defined here (last column)

State	State description	Compares to
0	Distal ends of terminal phalanges of fingers and toes simple, rounded, knob-like	State F
1	Distal ends of terminal phalanges of fingers and toes bifurcate (have a distinct median notch, state 2 of LIEM, 1970)	State M
2	Distal ends of terminal phalanges of fingers and toes rounded, but with lateral expansions, making the outline of the distal phalanx "mushroom-shaped" in appearance (no median notch)	State M
3	Distal ends of terminal phalanges of fingers simple, knob-like or as state 2, toes slightly T-shaped; the anterior distal border of the phalanx perpendicular to the axis (no median notch)	Reduced form of state H
4	Terminal phalanges of fingers and toes reduced, almost cone-like	State E
5	Fingers with expanded distal ends to terminal phalanges, phalanx appearing almost "dumbbell-shaped" (especially on third and fourth fingers); toes similar to state 4	State M
6	Distal ends of terminal phalanges of fingers and toes fairly pointed, curved dorsoventrally	States A and L

Table 3. Character states of terminal phalanx shape as used by DREWES (1984) (first column) and their equivalents as defined here (last column)

State	State description	Compares to
0	Terminal phalanx long, slender, and claw-shaped; curved ventrally and tapered evenly to a point.	Hook-shaped toe morphology
1	Terminal phalanx long, slender and peniform; a noticeable constriction present near tip; tip oval, but not pointed; phalanx may be slightly curved	Morphological group II (states E and F)
2	Terminal phalanx short, obtuse, and unmodified or with the tip slightly notched or emarginate	State M and morphological group I (states A and L), state M comprises different forms where the slightly notched morphology belongs; morphological group I can account for the unmodified tip
3	Tip bifurcate, each branch longer than width of phalanx just proximal to bifurcation	Morphological group III (state H)

morphology of state 2 compares to state M, whereas the unmodified tips fit state A and L (morphological group I). State 3 compares to morphological group III, more specifically to state H. Of the species categorized in state 0 by DREWES (1984), we studied *Heterixalus madagascariensis*, *Hyperolius argus*, *Leptopelis bocagii* and *L. modestus*. All were categorized in our state A, as well as other species studied within these genera. Of the species categorized in state 1 by DREWES (1984), we studied the following species: *Afrrixalus fornasini*, *A. fulvovittatus*, *Hyperolius nasutus*, *H. pusillus*, *H. tuberilinguis* and *Tachycnemis seychellensis*. Except for *Tachycnemis seychellensis*, which was categorized in our state M, all were categorized in our state A. Of the species categorized in state 2 by DREWES (1984), we studied *Kassina decorata*, which was placed in our state H, and *Phlyctimantis verrucosus*, which was placed in our state M. We did not study any of the species categorized in state 3 by DREWES (1984). We assume that the contradictions between the assignment of species to morphological states, between DREWES (1984) and our analysis, does not indicate true polymorphisms but are rather due to differences in interpretation.

SCOTT (2005) examined a large number of ranoid species osteologically and composed a data matrix of morphological and molecular characters for phylogenetic analysis. She distinguished between the terminal phalanx shape of the fourth finger and the fourth toe, defining three states within the finger morphology (tab. 4) and seven states within the toes (tab. 5). Here a comparison will be made for finger phalanx morphology.

State 0 of SCOTT (2005) is bifurcate, T- or Y-shaped, and compares to our morphological group III, which consists of states G, H, I, J and K. Of the taxa categorized in SCOTT's (2005) state 0, the following species were also analysed in the present study. *Natalobatrachus bonebergi*, *Batrachylodes vertebralis*, *Phrynobatrachus cricogaster*, *Phrynodon* cf. *sandersoni*, *Petropedetes* sp. [*P. cameronensis*, *P. natator*, *P. newtoni* and *P. parkeri* studied by SCOTT (2005)] and *Staurois* sp. [*S. natator* studied by SCOTT (2005)], all categorized in our state H, *Hylarana* (*Amnirana*) cf. *alohabris* and *Chiromantis xerampelma*, placed in our state J; *Phrynomantis bifasciatus*, placed in state G, tending to state J, *Phrynobatrachus natalensis* and *Hylarana* (*Hydrophylax*) *galamensis*, placed in our state M; *Mantella aurantiaca*, placed in our state I.

State 1 of SCOTT (2005) is knob-like and simple, and compares to our morphological group II, which consists of states E and F. Of the species categorized in SCOTT's (2005) state 1, the following species were also analysed in the present study. *Afrrixalus fornasini*, *Hyperolius marmoratus* and *Leptopelis* cf. *mossambicus*, placed in our state A; *Hemysus marmoratus*, *Breviceps mossambicus* and *Platymantis corrugatus*, placed in our state E; *Cucosternum boettgeri*, *Trichobatrachus robustus* and *Scotobleps gabonicus*, placed in our state F, although the latter two species showed a hook-morphology of toe phalanges; *Arthroleptis variabilis*, placed in our state M.

State 2 of SCOTT (2005) is sharply pointed and slightly elongated. The elongation compares to our state L, whereas the sharply pointed morphology matches the hook-shaped morphology found in the terminal phalanges of the toes (but not the fingers) of *Trichobatrachus robustus*, *Ptychadena bibrom*, *Astylosternus montanus*, *Scotobleps gabonicus* and *Silurana tropicalis*. Of the species categorized in state 2 of the finger morphology by SCOTT (2005), we studied *Ptychadena mascareniensis*, which we placed in state E, and *Strongylopus grayii* which we placed in state M.

Table 4 Character states of terminal phalanx shape of digit IV of hand as used by SCOTT (2005) (first column) and their equivalents as defined here (last column).

State	State description	Compares to
0	Bifurcate, T- or Y shaped	States G, H, I, J and K (morphological group III)
1	Knob-like, simple	States E and F (morphological group II)
2	Sharply pointed, slightly elongated	Elongated state L; sharply pointed: hook-shaped morphology

Table 5 Character states of terminal phalanx shape of digit IV of foot as used by SCOTT (2005) (first column) and their equivalents as defined here (but largely referring to fingers: last column).

State	State description	Compares to
0	Large T-shaped	State H
1	Small T- or Y-shaped	States G, H and (I)
2	Simple or only slightly dilated	State M
3	Long, sharply pointed	State N
4	Y-shaped, arms bearing flattened ovate flanges	State J
5	Pointed, truncated (short) to triangular, tip may be a small globule	States E and F
6	Long, sharply pointed, as in state 3, but tip separated from the body of terminal phalanx and bent sharply downwards (may or may not perforate the integument in life)	The extra hook separated from the rest of the phalanx, similar to the observation reported here in one specimen of <i>Trichobatrachus robustus</i>

SCOTT (2005) referred to *Phrynodon* having T-shaped tips (according to BLOMMERS-SC HLÖSSER, 1993), whereas she observed only Y-shaped tips herself. The SEM pictures in our study (fig. 5c-e) show a morphology in-between the two forms, with protuberances on top of the tips.

One further aspect that requires discussion is the identification reliability of the specimens studied. Many species of ranoids, especially small-sized African and Asian species, are notoriously difficult to identify to species, sometimes even to genus. We are confident in our identification of mantellid, brevipitid, microhylid and pyxicephalid species, but this is much less true for various phrynobatrachid, ptychadenid, arthroleptid or rhacophorid taxa, several of which were obtained from the pet trade without verified locality data. Genus attribution of all specimens studied herein is reliable, and possible misidentifications will not affect our major conclusions. However, when comparing detailed data for single species among studies, this potential source of error, in our study as well as in published works, needs to be considered.

HOMOPLASY AND ECOLOGICAL CORRELATES OF PHALANX MORPHOLOGY

Several authors have reported differences between phalanges of fingers and toes, and also among fingers or toes. DREWES (1984) found little variation in this respect in the species examined, but restricted his analysis to the third finger based on the work of HEYER (1975) in hylid frogs at the time considered to be in the family Leptodactylidae (now partitioned; FROST et al., 2006). HEYER (1975) found variation of terminal phalanx shape from digit to digit. CLARKE (1981) has also noted that the phalanx morphology on toes and fingers does not necessarily correspond to each other. Any one of the states he distinguished varies in degree on the different digits of a limb. He noted that in general a given state is best expressed on the third and fourth fingers on the hand, and the third, fourth and fifth toes on the foot. Our observations confirm that the general phalanx morphology of a species is best expressed in the longest digits available, which usually are the third finger and the fourth toe.

Altogether the comparisons reported above indicate that scoring character states of terminal phalanx shape in frogs is a difficult endeavour, and along with FABREZI (1996) we conclude that this character is strongly affected by homoplasy. The number of states distinguished appears to depend on which groups of ranoids are studied, and certainly is also affected by subjective decisions of the different researchers. LIEM (1970) focused on rhacophorids, mantellids and hyperolids, with some additional taxa as outgroups, and distinguished four states; DREWES (1984) studied mainly hyperolids and leptopelinae, and distinguished four states; CLARKE (1981) studied representatives of microglossids, psychadenids, pyxicephalids and microglossids, and distinguished seven states. SCOTT (2005) studied most lineages of ranoids and distinguished three character states for finger phalanx shape, and seven character states for toe phalanx shape. In the present study we used SEM to better visualize the phalanx morphology and partly arrived at categorizations different from those of previous workers. However, in many cases, especially when terminal structures are weakly expressed, it is very difficult to provide a clear categorization and distinction between clear-cut states, a dilemma also noted by CLARKE (1981) and FABREZI (1996). In addition, ontogenetic artefacts may more commonly have the power to obscure genetically determined (and hence phylogenetically relevant) underlying morphology in such "reduced" states where the diagnostic shape is not marked by distinctive protruding elements. We do not expect sexual dimorphism to occur in this and most other osteological characters, but such a potential influence remains largely unstudied. For these methodological reasons alone, and in line with the conclusion of CLARKE (1981), the value of the morphology of terminal phalanges to infer phylogenies must be seen as very limited.

A further issue is whether terminal phalanges undergo rapid adaptive modifications and can therefore mask rather than resolve phylogenetic relationships. Several authors correlated terminal phalanx morphology with habitat and habits. DREWES (1984) hypothesized that this character can be explained by the frog's habitat, and that the different states may constitute specialisations for muscle insertions. LIEM (1970) noted that modifications of the terminal phalanx were present in most arboreally adapted species, and CLARKE (1981) assumed that terminal phalanges often undergo adaptive modifications.

The survey and comparative analysis presented here indicate, on one hand, an important phylogenetic component in terminal phalanx morphology. For example, all species of the

subfamilies Boophinae and Mantellinae in the family Mantellidae examined (LIEM, 1970; VENCES et al., 2002; our data) have a similar, slightly Y-shaped bifurcated phalanx shape (our state 1), although the Mantellidae are a rather old group that probably split from the Rhacophoridae in Cretaceous to Paleocene times (BOSSUYT & MILINKOVITCH, 2001; VENCES et al., 2003), and although especially mantellines are ecologically and morphologically very diverse, containing climbing as well as largely terrestrial frogs (GLAW & VENCES, 2006). A similar case can be made for several other groups, such as the Hyperolidae which almost all have non-bifurcated phalanges. A phylogenetic component is also obvious from the fact that several character states were identified in the few non-ranoid taxa examined here which were not found in any of the vast number of ranoids studied.

On the other hand, our data also provide the first significant evidence for shifts in phalanx morphology in concert with shifts in habits of the frogs. Such an analysis is made difficult by the plethora of different character states observed. We therefore decided to study a single pattern, terminal bifurcation of phalanx, where a reasonable working hypothesis could be drawn and tested: arboreal and rock dwelling climbing frogs have usually evolved (phylogenetically independently; OHLFR & DU BOIS, 1989) enlarged disks of fingers and toes, and an enlarged terminal phalanx may be useful as internal support for this disk, or as attachment for muscles that increase disk mobility for improved climbing. A correlation of these characters with the presence of an intercalary element between terminal and subterminal phalanges of fingers and toes, and of this element with climbing habits, has already been found by MANZANO et al. (2007). By coding terminal phalanx shape and habits each as binary characters (terminal enlargement of phalanx by bifurcation, vs. no such distinct enlargement; and climbing vs. not climbing) we could apply a statistical test and reject a stochastic distribution of both characters along the phylogeny. This indicates that indeed terminal phalanx bifurcation evolved multiple times in concert with climbing behaviour, but more sophisticated analyses are necessary to better understand this evolutionary process. Since bifurcation differs in several metric variables (angle of protrusion of lateroterminal processes, and their length and width), and arboreal and rock-dwelling frogs differ in the degree of climbing (e.g., some scansorial frogs climb only at night whereas other frogs leave the trees only for breeding), it is in principle possible to perform a quantitative comparative analysis along a phylogeny. Other factors could be taken into account by multivariate approaches, such as the size of the terminal finger disks, the presence of intercalary elements and the structure of digit muscles, which may functionally correlate with terminal phalanx shape (MANZANO et al., 2007). We are convinced that more in-depth descriptive studies of morphological character states in combination with character tracing along well-supported molecular phylogenies will be highly informative to understand their ecological correlates and adaptive value. Along with SCOTLAND et al. (2003), but acknowledging the criticisms of JENNER (2004) and WILMS (2004) to a generalization of this approach, we believe in the usefulness of detailed analysis of particular morphological characters, in this case in anuran osteology. In contrast to uncritical studies that aim to add a maximum number of morphological characters to data matrices for phylogenetic analyses, such detailed and focused morphological analyses are more promising. They are required to identify diagnostic and phylogenetically informative characters for major anuran clades which are badly needed to reliably assign fossil forms to evolutionary lineages. And they will contribute to the long-neglected field of anuran functional anatomy by drawing hypotheses on possible adaptive significances of particular character states.

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APPENDIX

List of specimens studied. Collection abbreviations are as follows. Musco Regionale di Scienze Naturali, Torino (MRSN), Museum National d'Histoire Naturelle, Paris (MNHN), Museum of Comparative Zoology, Cambridge (MCZ, housed as exchange in ZSM); Zoologisch Museum Amsterdam, Amsterdam (ZMA), Zoologische Staatssammlung München, München (ZSM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Thomas Ziegler working collection (TZ; specimens to be included in ZFMK). Other abbreviations used. SEM, examined by Scanning Electron Microscope, MIC, examined by stereo microscope (and in most cases schematically drawn with the aid of a camera lucida). Character states as used and explained in the text.

Species	Catalogue number	SEM/MIC	Character state
RANID FAMILIES			
<i>ARTHROLEPTIDAE</i> Mawat, 1869. <i>ARTHROLEPTINAE</i> Mawat, 1869			
<i>Arthroleptus subdiffidens</i> Nieden, 1911	ZFMK 58906	MIC	M
<i>Arthroleptus poeyi domus</i> Peters, 1863	ZFMK 61383, ZFMK 67497	MIC	M
<i>Arthroleptus</i> sp.	ZFMK 68794	MIC	M
<i>Arthroleptus variabilis</i> Mulsant, 1893	ZFMK 28960	MIC	M
<i>Arthroleptus</i> ? <i>h. h. h.</i> sp.	MNHN 1979 3852	MIC	H
<i>ARTHROLEPTIDAE</i> Mawat, 1869. <i>ARTHROLEPTINAE</i> Nüble, 1927			
<i>Artylasteria montana</i> Arnet, 1978	ZFMK 67732	MIC	F
<i>Lepidoleptus lucidus</i> Perret, 1959	ZFMK 67746	MIC	A
<i>Scintillipes gubianae</i> Boulogne, 1900	ZFMK 61330, ZFMK 67755	MIC	Finger F, toe hook morphology
<i>Trichobatrachus rubrivittatus</i> Boulogne, 1900	ZFMK 68850-68851	SEM, MIC (toe), MIC (finger)	Finger F, toe hook morphology
<i>ARTHROLEPTIDAE</i> Mawat, 1869. <i>LEPTOLEPTINAE</i> Laurent, 1972			
<i>Leptoleptus bogarti</i> (Günther, 1865)	ZFMK 68787-68788	MIC	A
<i>Leptoleptus cf. amoenus</i> Puyntun, 1985	ZFMK 29644	MIC	A
<i>Leptoleptus mulsanti</i> (W. em., 1898)	ZFMK 67412	MIC	A
<i>Leptoleptus notolensis</i> (Smith, 1849)	ZFMK 68783 (juvenile), 68784, 68785	MIC	A
<i>Leptoleptus notolensis</i> (Smith, 1849)	ZFMK 68785	SEM, MIC	A
<i>Leptoleptus ruber</i> Reichenow, 1874	ZFMK 67992	MIC	A
<i>BREVICOPTIDAE</i> Bonaparte, 1850			
<i>Brevicoptis fuscus</i> Hewitt, 1925	ZFMK 68848	MIC	F
<i>B. sp.</i>	ZFMK 68849	SEM, MIC	
<i>CEPHALOTRACHIDAE</i> Boulogne, 1894			
<i>Batrachobatrachus elegans</i> Brown & Parker, 1970	MCZ A 39279 (ZSM 21, 393, MCZ A 78281) (ZSM 21 1996)	MIC	H
<i>Batrachobatrachus trichobatus</i> Boulogne, 1897	MCZ 7 44143	MIC	H
<i>Cephalotrachus giesbreghtii</i> Boulogne, 1894	ZFMK 50183	SEM, MIC	F
<i>Phrynosoma curvicauda</i> (Duméril, 1853)	ZFMK 63644	SEM, MIC	F
<i>DIAPYCNIDAE</i> Anderson, 1871			
<i>Diapycnis ephelocypis</i> (Peters, 1863)	ZFMK 42842	MIC	F
<i>Fegernaria camerunensis</i> (Gravenhorst, 1829)	ZFMK 20364	SEM, MIC	A or F
<i>Fegernaria lamprochroa</i> (Gravenhorst, 1829)	TZ 526, ZFMK 49215	MIC	A or F
<i>Hoplodactylus olivaceus</i> (Osbeck, 1765)	TZ 385	MIC	E
<i>Lomaxotus kahle</i> (Schubert, 1838)	TZ 519	MIC	F
<i>Nomophis petersi</i> Günther, 1896	ZFMK 58098	MIC	I
<i>N. sp.</i>	ZFMK 68825, ZFMK area oligoneura	MIC	A
<i>Phrynosoma marmoratus</i> (Peters, 1867)	TZ 155	MIC	I
<i>Phrynosoma spinosum</i> (Duméril, 1875)	ZFMK 9719	MIC	F
<i>Phrynosoma brevicauda</i> (Schneider, 1799)	ZFMK 13796, ZSM 70 1979	MIC	F
<i>DIPIPTERIDAE</i> Cope, 1867			
<i>Dipipterus marmoratus</i> (Peters, 1854)	ZFMK 68848 (juvenile)	MIC	I

Species	Catalogue number	SEM/ MIC	Character state
<i>HYPEROLIDAE</i> Laurent 1943			
<i>Afrizalus delicatus</i> Pickering, 1864	ZFMK 68792	MIC	A
<i>Afrizalus formosus</i> (Bancroft, 1849)	ZFMK 68789	MIC	A
<i>Afrizalus fulvovittatus</i> (Cope, 1861)	ZFMK 62576	MIC	A
<i>Afrizalus</i> sp.	ZFMK uncatalogued	SEM, MIC	A
<i>Afrizalus</i> sp.	ZFMK 68790-68791	MIC	A
<i>Afrizalus</i> sp.	ZFMK uncatalogued	MIC	A
<i>Heterizalus uliginosus</i> (Boettger, 1882)	ZFMK 68793	MIC	A
<i>Heterizalus andrakata</i> Gaw & Venes, 1991	ZFMK 52561, 52564	MIC	A
<i>Heterizalus beslei</i> (Granddier, 1872)	MRSN A.399 4, ZMA 6724, 6796, ZMA FN 995	MIC	A
<i>Heterizalus latrostratus</i> (Andersson, 19 0)	MRSN A 393 7	MIC	A
<i>Heterizalus madagascariensis</i> (Duméril & Bibras, 1841)	ZFMK 52574, 52647	MIC	A
<i>Heterizalus punctatus</i> Gaw & Venes, 1994	ZFMK 60018	MIC	A
<i>Heterizalus rutenbergi</i> (Boettger, 1881)	ZFMK 59844	MIC	A
<i>Heterizalus tricolor</i> (Boettger, 1881)	ZFMK 52583	MIC	A
<i>Heterizalus variabilis</i> (Ahl, 1930)	ZFMK 52578, 53606	MIC	A
<i>Hyperolius argus</i> Peters, 1854	ZFMK 68780	MIC	A
<i>Hyperolius marmoratus</i> Rapp. 1842	ZFMK 68773-68777, ZFMK uncatalogued 12 specimens	MIC	A
<i>Hyperolius nasutus</i> Günther, 1865	ZFMK 68782	MIC	A
<i>Hyperolius pusillus</i> (Cope, 1862)	ZFMK 68781	MIC	A
<i>Hyperolius semidiscus</i> Hewitt, 1927	ZFMK 68779	MIC	A
<i>Hyperolius</i> sp.	ZFMK uncatalogued	MIC	A
<i>Hyperolius roberilougus</i> Smith, 1849	ZFMK 68778	MIC	A
<i>Kassia decorata</i> (Angel, 1940)	ZFMK 67841	MIC	H
<i>Phyllomantis verrucosus</i> (Boettger, 1912)	ZFMK 58824	MIC	M
<i>Tachyomantis zeyheri</i> (Duméril & Bibras, 1841)	ZFMK 62859, 62879	MIC	M
<i>MANTHOLIDAE</i> Laurent 1946			
<i>Aglyptodactylus madagascariensis</i> (Duméril, 1853)	ZFMK 18954	SEM, MIC	F
<i>Aglyptodactylus madagascariensis</i> (Duméril, 1853)	ZFMK 52682, 60889	MIC	E
<i>Bombomera witteri</i> (Guibé, 1974)	ZFMK 53594	MIC	I
<i>Boreophis boehmei</i> Gaw & Venes, 1992	ZFMK 56651	MIC	I
<i>Boreophis cf. madagascariensis</i> (Peters, 1874)	MRSN	MIC	I
<i>Boreophis olva</i> (Stenardacher, 1867)	ZFMK 53649	MIC	I
<i>Boreophis mesasiaticus</i> (Mocquard, 1902)	ZFMK 48166	MIC	I
<i>Boreophis</i> sp. aff. <i>subulana</i>	ZFMK 62797	MIC	I
<i>Boreophis tephrocassina</i> (Duméril, 1853)	ZFMK 68810	SEM	I
<i>Boreophis tephrocassina</i> (Duméril, 1853)	ZFMK 68811	SEM, MIC	I
<i>Cephalomantis webbi</i> (Grandson, 1953)	ZFMK 52726	MIC	I
<i>Gubermantia bicoloratus</i> (Boettger, 1913)	ZFMK 8877	MIC	I
<i>Gubermantia flavobrunnea</i> (Blommers-Schlösser, 1979)	ZFMK 17621	MIC	I
<i>Lobulostoma labrossei</i> (Cope, 1868)	ZMA FN 73, ZFMK 52755, 59965	MIC	F
<i>Lobulostoma labrossei</i> (Cope, 1868)	ZFMK 8890, 59967	SEM, MIC	F
<i>Mantella mantelliana</i> Mocquard, 1900	ZFMK 68807	MIC	I
<i>Mantella crocea</i> Ponce & Bohne, 1990	ZFMK 68806	MIC	I
<i>Mantella madagascariensis</i> (Granddier, 1872)	ZFMK 68808	MIC	I
<i>Mantodactylus albopunctatus</i> (Müller, 1892)	ZFMK 25373	MIC	I
<i>Mantodactylus granddieri</i> Mocquard, 1895	MRSN	MIC	I
<i>Mantodactylus uliginosus</i> (Boettger, 1880)	ZFMK 68805	SEM, MIC	I
<i>Phyllomantis aglaei</i> (Méthuen & Hewitt, 1913)	ZFMK 46021	MIC	I
<i>MICROTILIDAE</i> Günther 1858			
<i>Amphidactylus nanus</i> Angel, 1925	MNHN 1972 1112	SEM, MIC	G
<i>Callisiba guineana</i> (Blyth, 1856)	ZFMK 40 45	MIC	I
<i>Cophosaurus darlingtoni</i> (Laverdige, 1946)	MIC 71561-71562	MIC	H
<i>Cophosaurus sparvus</i> Zweifel, 1962	MIC 2 20189, 20196	MIC	H
<i>Cophyla phyllodactyla</i> Boettger, 1880	ZFMK 68846	MIC	G
<i>Dermatomantis maellieri</i> (Boettger, 1885)	ZFMK 40975	MIC	I
<i>Gastrophyscia cf. ovata</i> (Hallowell, 1856)	ZFMK 68845	SEM, MIC	M
<i>Kalohyla pulchra</i> Gray, 1833	ZFMK 6462	MIC	(H, F, M, G, I)
<i>Microrhina pulchra</i> (Hallowell, 1861)	TZ 530	MIC	F

Species	Catalogue number	SEM MIC	Character state
<i>MICROTHYLIDAE</i> Götlicher, 1858 (continuation)			
<i>Phrynosomus bifasciatus</i> (Smith, 1847)	ZFMK 68843	SEM, MIC	G (tends to J)
<i>Phrynosomus bifasciatus</i> (Smith, 1847)	ZFMK 68844	MIC	G (tends to J)
<i>Phrynosomus mucropus</i> Peters, 1875	ZFMK 68842	SEM, MIC	G (tends to J)
<i>Scaphisphryne brevis</i> (Boulenger, 1896)	MNHN 1975 2612	SEM, MIC	E
<i>Scaphisphryne calcarata</i> (Mooquard, 1895)	ZFMK 59998	SEM, MIC	F
<i>Scaphisphryne macronota</i> Boulenger, 1892	ZFMK 50150	MIC	H
<i>PETROPHIDAE</i> Nohle, 1931			
<i>Petrophidius</i> sp.	MNHN 1989 3999	SFM (3B), MIC	H
<i>PHYRINOBATRACHIDAE</i> Laurent, 1941			
<i>Phrynobatrachus auratus</i> Boulenger 1900	ZFMK 64261	MIC	G
<i>Phrynobatrachus cf. versicolor</i> Ahl, 1924	ZFMK 58788	MIC	H/M
<i>Phrynobatrachus cricogaster</i> Perret, 1957	ZFMK 67299	MIC	H
<i>Phrynobatrachus mohabensis</i> Faiz Simons, 1932	ZFMK 68821	SF M (toe IV), MIC	M
<i>Phrynobatrachus mohabensis</i> Faiz Simons, 1932	ZFMK 68822	MIC	M
<i>Phrynobatrachus natalensis</i> (Smith, 1849)	ZFMK 68816-68817, 688 9-68820	MIC	M
<i>Phrynobatrachus natalensis</i> (Smith, 1849)	Z+MK 68818	SEM finger I, I), M,C	M
<i>Phrynobatrachus werneri</i> (Nauden, 1910)	ZFMK 68033	SF M (toe IV), M,C	Finger M (tends to H; toe IV M)
<i>Phrynobatrachus cf. werneri</i> (Nauden, 1910)	ZFMK 47960, 47992	MIC	H or M
<i>Phrynosoma cf. sandersoni</i> (Parker, 1935)	ZFMK 67342, 68253, 68257	M,C	H
<i>Phrynosoma cf. sandersoni</i> (Parker, 1935)	ZFMK 68 79	SF M MIC	H
<i>PTYCHADENIDAE</i> Dubois, 1907			
<i>Ptychadena bibroni</i> (H. A. J. Boulenger, 1845)	ZFMK 15420	MIC	E
<i>Ptychadena bibroni</i> (H. A. J. Boulenger, 1845)	Z+MK 17017	M,C	Finger E, toe hook morphology
<i>Ptychadena schubertiana</i> (Werner, 1908)	ZFMK 34045	MIC	F
<i>Ptychadena macranemata</i> (Duméril & Bibron, 184)	ZFMK 55 57	SF M, MIC	Finger E, toe A, tending towards hook morphology
<i>Ptychadena macranemata</i> (Duméril & Bibron, 184)	ZFMK 55621	MIC	E
<i>Ptychadena cf. macranemata</i> (Duméril & Bibron, 1841)	ZFMK 68826-68827	MIC	E
<i>PEZICOPHIDAE</i> Bonaparte, 1850			
<i>Cucosternum boettgeri</i> (Boulenger, 1882)	ZFMK 33 16	MIC	F
<i>Cucosternum boettgeri</i> (Boulenger, 1882)	ZFMK 33 17	SEM, MIC	F
<i>Natalobatrachus bonebergi</i> Hewitt & Methuen, 1912	ZFMK 68812	SF M MIC	H
<i>Natalobatrachus bonebergi</i> Hewitt & Methuen, 1912	ZFMK 68813-68814	MIC	H
<i>Stromatoporus gravis</i> (Smith, 1849)	ZFMK 33097	SF M, MIC	M
<i>Tomopterna delalandei</i> (Tschudi, 1838)	ZFMK 44598	M,C	F
<i>Tomopterna natalensis</i> (Smith, 1849)	ZFMK 33 64, 68815	M,C	F
<i>PHYLLOPHIDAE</i> R. F. Ingersoll, 1914			
<i>Phyllorhina (Anaxyrus) cf. albifacies</i> (Hallanell, 1856)	MNHN 1989 4151	M,C	J
<i>Phyllorhina (Anaxyrus) levis</i> (Anderson, 1903)	ZFMK 64830	M,C	M
<i>Phyllorhina (Phyllorhina) galamensis</i> (Duméril & Bibron, 184)	ZFMK 61676	SF M MIC	M
<i>Phyllorhina (Phyllorhina) macrodactyla</i> G. Oelher, 1859	TZ 667 ZFMK 43956	MIC	M
<i>Phyllorhina (Phyllorhina) nigrovittata</i> (Blyth, 1856)	TZ 67, 756	MIC	M
<i>Phyllorhina eustrebanus</i> (Sikow, 1902)	ZFMK uncatalogued (2 juveniles)	M,C	F
<i>Oedipina livida</i> (Blyth, 1856)	TZ 349	M,C	M
<i>Oedipina livida</i> (Blyth, 1856)	TZ 527	SF M, MIC	M
<i>Rana chalybeata</i> Boulenger in Bonaparte, 1838	ZFMK 68824	MIC	M
<i>Rana temporaria</i> Linnaeus, 1758	ZFMK uncatalogued	M,C	M
<i>Siamia</i> sp.	ZFMK 16597	SF M M,C	H
<i>Siamia</i> sp.	ZFMK 16598	MIC	H
<i>PHYLLOPHIDAE</i> (continued)			
<i>Chironomantis variegata</i> Peters, 1854	ZFMK 29467	MIC	J
<i>Chironomantis variegata</i> Peters, 1854	ZFMK 68795	SF M MIC	J
<i>Acanthodes verrucosus</i> (Boulenger 1893)	TZ 444	MIC	I
<i>Polypedates eylesi</i> Günther 1858	ZFMK 68797, 68799	MIC	G
<i>Polypedates eylesi</i> Günther 1858	ZFMK uncatalogued (5 spec. 1893)	MIC	G

Species	Catalogue number	SEM/ MIC	Character state
RHACOPHYRIDAE Hofman, 1932 (combination)			
<i>Polyspates maculatus</i> (Gray, 1830)	ZFMK 13784-13785	MIC	G
<i>Polyspates oriolophus</i> (Bouvier, 1893)	ZFMK 68852	SEM, MIC	G
<i>Rhacophorus deanyis</i> Blanford, 1881	ZFMK 65461	SEM, MIC	G
<i>Rhacophorus nepalensis</i> Bouvier, 1895	ZFMK uncatalogued	MIC	G
NON-RANDID FAMILIES			
BOBRINATRIDAE Gray, 1825			
<i>Bombus</i> sp.	ZFMK uncatalogued	MIC	F
CENTROLEPIDAE Taylor, 1951			
<i>Hyalinobatrachium Reichmanni</i> (Boettger, 1893)	ZFMK 68768	SEM, MIC	K
DENDROBATILAE Cope, 1865			
<i>Amerioba oberstonei</i> (Myers & Daly, 1979)	ZFMK 40709, 68828	MIC	H
<i>Colastes subicola</i> (Dunn, 1924)	ZFMK 46644	MIC	H
<i>Dendrobates auratus</i> (Günther, 1855)	ZFMK 68807	MIC	H
<i>Dendrobates leuconotus</i> Steindachner, 1864	ZFMK 68839	MIC	H
<i>Dendrobates tinctorius</i> (Lacaze, 1797)	ZFMK 68838	MIC	H
<i>Epiplatobates boulengeri</i> (Barbour, 1909)	ZFMK 68829	MIC	H
<i>Oophaga lehmanni</i> (Myers & Daly, 1976)	ZFMK 68834	MIC	H
<i>Oophaga pumilio</i> (Schmidt, 1857)	ZFMK 68836	MIC	H
DIPLOGLOSSIDAE Günther, 1858			
<i>Dicoglossus cf. galgano</i> Capula, Nascetti, Lanza, Bullini & Crespo, 1985	ZFMK uncatalogued	MIC	b
<i>Dicoglossus monticola</i> Lanza, Nascetti, Capula & Bullini, 1984	ZFMK uncatalogued	MIC	M
<i>Dicoglossus sardus</i> Tschudi in Orb, 1837	ZFMK uncatalogued	MIC	M
HELLEOPHYRIDAE Noble, 1931			
<i>Helleophrys rugis</i> Hewitt, 1910	ZFMK 68769-68771	MIC	G
HYLIDAE Rafinesque, 1815			
<i>Agalychnis callidryas</i> (Cope, 1862)	ZFMK uncatalogued	SEM, MIC	L
<i>Hyla arborea</i> (Linnaeus, 1758)	ZFMK 68766	MIC	E
<i>Hyla cinerea</i> (Schneider, 1799)	ZFMK uncatalogued	MIC	E
<i>Phyllomedusa sauvagii</i> Bouvier, 1882	ZFMK uncatalogued	MIC	A
MEGALOPHYRIDAE Bonaparte, 1850			
<i>Megalophrys nasuta</i> (Schlegel, 1858)	ZFMK 68853	MIC	A
MIBOMBATRIDAE Schlegel, 1850			
<i>Limonectes</i> sp.	ZFMK uncatalogued	MIC	D
<i>Pseudohyla hebraea</i> Günther, 1859	ZFMK 28-59	SEM, MIC	E
PYLIDAE Gray, 1825			
<i>Hemiocharis boettgeri</i> (Tomes, 1896)	ZFMK uncatalogued	SEM, MIC	L
<i>Pipa carvalhoi</i> (Miranda-Ribeiro, 1937)	ZFMK uncatalogued	SEM (loc), MIC (Fig. 2, 3, 10)	Finger B, toe E
<i>Sitarona tropiculus</i> Gray, 1864	ZFMK uncatalogued	MIC	N
<i>Ventanus vicarinus</i> AHL, 1924	ZFMK uncatalogued	SEM, MIC	C
CYLOGLISSIDAE Bonaparte, 1850			
<i>Rhinoderma darwini</i> Duméril & Bibras, 1841	ZFMK 68767	MIC	M